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Stand-replacing wildfires increase nitrification for decades in southwestern ponderosa pine forests

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Abstract Stand-replacing wildfires are a novel disturbance within ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States, and they can convert forests to grasslands or shrublands for decades. While most research shows that soil inorganic N pools and fluxes return to pre-fire levels within a few years, we wondered if vegetation conversion (ponderosa pine to bunchgrass) following stand-replacing fires might be accompanied by a long-term shift in N cycling processes. Using a 34-year stand-replacing wildfire chronosequence with paired, adjacent unburned patches, we examined the long-term dynamics of net and

gross nitrogen (N) transformations. We hypothesized that N availability in burned patches would become more similar to those in unburned patches over time after fire as these areas become re-vegetated. Burned patches had higher net and gross nitrification rates than unburned patches ($P < 0.01$ for both), and nitrification accounted for a greater proportion of N mineralization in burned patches for both net ($P < 0.01$) and gross ($P < 0.04$) N transformation measurements. However, trends with time-after-fire were not observed for any other variables. Our findings contrast with previous work, which suggested that high nitrification rates are a short-term response to disturbance. Furthermore, high nitrification rates at our site were not simply correlated with the presence of herbaceous vegetation. Instead, we suggest that stand-replacing wildfire triggers a shift in N cycling that is maintained for at least three decades by various factors, including a shift from a woody to an herbaceous ecosystem and the presence of fire-deposited charcoal.

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Introduction

Complex interactions between land management and climate change have led to pronounced changes in the wildfire disturbance regimes of coniferous forests throughout the western United States (US; McKenzie et al. 2004; Williams et al. 2010). Wildfire is the most pervasive natural disturbance in these ecosystems (Agee 1998), and a century of fire exclusion, coupled with a warmer and drier climate, have led to widespread build-ups in fuel loadings, as well as increases in the frequency and size of stand-replacing wildfires throughout this region (Covington and Moore

1994; Westerling et al. 2006). Severe fires can alter plant community structure (Hebel et al. 2009), primary productivity (Sabo et al. 2008), microbial communities (Smithwick et al. 2005), and the biogeochemical cycling of carbon (C; Kashian et al. 2006) and nitrogen (N; DeLuca et al. 2002; Turner et al. 2007). Some coniferous forests are adapted to high-severity wildfires (e.g., jack pine, *Pinus banksiana* Lamb., and lodgepole pine, *Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson), but others, such as southwestern ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm), are adapted to low-intensity surface fire regimes (Cooper 1960). For these forests, the relatively common occurrence of high-severity fires over the last ~40 years (Covington et al. 1997) constitutes a major shift in their natural disturbance regime. The frequency of stand-replacing wildfires is predicted to increase in the western US (Westerling et al. 2006), but the long-term implications of a disturbance regime shift on ecosystem functioning are uncertain.

The effects of stand-replacing wildfires on N cycling dynamics are of particular interest because N, along with water, is limiting to cone production and diameter growth in southwestern ponderosa pine forests (Heidmann et al. 1979; Heidmann 1984). Accordingly, post-fire N availability may be critical to pine regeneration and net primary productivity. Historically, the relatively rapid turnover of N was the result of a frequent, low-intensity surface fire regime, which maintained the forest structure in uneven-aged groups with abundant herbaceous openings (Cooper 1960; White 1985). Hart et al. (2005) hypothesized that this vegetation structure influenced the belowground microbial community, which, in turn, promoted rapid N cycling. However, fires in this region were virtually eliminated by practices introduced by Euro-American settlers in the late 1800s: livestock grazing reduced herbaceous fuels that would carry a surface fire, and active fire suppression led to extended periods of fire exclusion (Covington et al. 1997). Current forests are characterized by high densities of small diameter trees (Covington and Moore 1994), and associated net N transformation rates are less than half that of the historic regime, as suggested by forest restoration treatments (Kaye and Hart 1998a).

Although fires result in a loss of organic N stored in biomass (Johnson et al. 2005), they also initiate a temporary pulse in available N in the soil, which may facilitate post-fire regeneration (White 1986; Covington and Sackett 1992). This pulse is initially comprised of pyrogenically produced ammonium (NH_4^+), which remains high for approximately 1–2 years following fire (Raison 1979; Turner et al. 2007). Increased concentrations of nitrate (NO_3^-) follow the NH_4^+ pulse as nitrification is enhanced by higher substrate availability (NH_4^+ ; Robertson and Vitousek 1981), higher soil temperature and pH

(Christensen 1973; Bauhus et al. 1993), and the presence of fire-deposited charcoal (DeLuca and Sala 2006). Elevated levels of NO_3^- reach their maximum approximately 1 year after prescribed burning (Wan et al. 2001). Nitrogen availability may decline over secondary succession as plant–microbial competition for N increases (Kaye and Hart 1997) and regenerating vegetation alters the soil microclimate (Vitousek et al. 1989).

Despite the multitude of studies that have been conducted on the short-term N cycling responses to wildfire, there is comparatively little known about the long-term (years to decades) effects. Long-term declines in inorganic N availability over time since stand-replacing wildfires have been reported in northern boreal forests (DeLuca et al. 2002) and lodgepole pine forests (Turner et al. 2007), while increases have been observed in jack pine (Yermakov and Rothstein 2006) and southern boreal forests (Brais et al. 1995). Notably, all of these long-term studies occurred in forests that are adapted to stand-replacing fire regimes.

Unlike ecosystems that are adapted to stand-replacing fire disturbance (e.g., boreal forest, lodgepole pine), post-fire ponderosa pine regeneration is slow and variable (Savage and Mast 2005; Crotteau et al. 2013), which can cause burned forests to remain in grass- or shrub-dominated states for extended periods (Roccaforte et al. 2012). This state-shift may favor a prolonged post-fire enhancement of inorganic N availability and net N transformations by maintaining higher soil temperatures and pH and limiting plant uptake of N compared to unburned forests. Conversely, stand-replacing wildfires are associated with long-term reductions in soil C in these systems (Ross et al. 2012); this may limit microbial activity and constrain gross production of NH_4^+ over time (Koyama et al. 2010).

Our objective was to assess the effects of a novel disturbance, stand-replacing wildfires, on N cycling dynamics in southwestern ponderosa pine forests. We measured N availability (inorganic N pools and net N transformation rates) and gross N production rates along a wildfire chronosequence. Each burned area (patch) was paired with an adjacent area (patch) in unburned forest to better isolate the effects of time after fire. We hypothesized that N availability would initially be high following stand-replacing wildfires, but, as secondary succession proceeds and vegetation demand for N increases, availability would decline over time, eventually resembling that of comparable unburned forests. We predicted that elevated rates of nitrification would drive increases in N availability in burned patches, and that differences between burned and unburned patches would be more pronounced during the summer monsoon season (early July to mid-September) when biological activity is maximized. We also hypothesized that gross nitrification rates would decline over time after fire because of decreases in substrate availability, soil temperature, and

soil pH, as well as the declining effect of charcoal inputs occurring over succession. Conversely, gross N mineralization rates would increase over time after fire as initial C limitations resulting from combustion (Koyama et al. 2010; Ross et al. 2012) would be ameliorated by increasing C inputs from plant litter (Turner et al. 2007). Both gross N production rates would eventually resemble those of comparable unburned forest (Davidson et al. 1992).

Materials and methods

Study sites and experimental design

We conducted this study across seven post-wildfire sites in ponderosa pine forests of northern Arizona, US. Sites were located on basaltic parent material and each had experienced one stand-replacing crown fire (>95 % tree mortality) within the last 60 years according to records at Coconino and Kaibab National Forests (Table 1). The Fort Valley weather station (within 23 km and at a similar elevation to all sites) received 65.4 cm of precipitation during the 12-month study period (1 July 2007–1 July 2008; www.wrcc.dri.edu). The mean daily maximum and minimum air temperatures for the same period were 17.2 and -3.7 °C, respectively. The 30-year averages (1971–2000) for the station were 56.3 cm/year of precipitation, with mean daily maximum and minimum air temperatures of 16.3 and -3.6 °C, respectively. Approximately half of the precipitation falls in the form of snow during the winter months, while the remainder falls as rain during the summer monsoon season (early July to mid-September).

We employed a chronosequence (space-for-time substitution) approach to examine the long-term effects of stand-replacing wildfires. We sampled a broad temporal extent (seven sites over a 34-year period) rather than replicating sites over a smaller number of years because this design was better suited to illustrate changes in N cycling dynamics over time. Each site consisted of a burned patch paired with an adjacent patch of unburned forest to better isolate the effects of fire from other sources of variation (Johnson and Miyanishi 2008). We recognize that the chronosequence approach has lower inferential power than a true experiment, and we note that conclusions derived from the results are based on the assumption that burned patches and their paired unburned patches were similar prior to the fire. Additionally, two of the older wildfire sites (23 and 34 years-after-fire) were salvage logged and replanted after the fire, which was the typical management practice at the time (the other sites did not receive active post-fire management). While this management difference also limits our study design, we felt that the need for a clearer understanding of long-term post-wildfire ecosystem functioning,

coupled with the limited number of suitable wildfire sites in this region, justified the inclusion of these older sites. Furthermore, a companion study performed at this chronosequence found that pools of C and N (live plant biomass and woody debris C; mineral soil and organic horizon C and N) remained relatively constant with time after fire (Ross et al. 2012), suggesting that the management did not substantially compromise the chronosequence.

At each burned patch, we established three 300-m transects within the perimeter of the burn. Similarly, we established transects in the paired unburned patches. Burn area heterogeneity prevented identical transect orientation and layout across all the sites, but we attempted to sample in a similar manner as much as possible; this included covering a similar areal extent at all the burned and unburned patches. Three 10-m-radius plots were located 150 m apart along each of the three transects for a total of nine plots at each patch ($n = 9$). Plots were at least 100 m from active roads and 20 m from trails or old logging roads. At most of the burned patches, transects were at least 100 m from unburned forest; however, at the two most recent burns (2 and 6 years-after-fire), the size and perimeter of the burn meant that several plots were as little as 25 m from unburned forest. Table 1 presents basic soil and vegetation characteristics.

Quantification of net N mineralization rates

We measured in situ net N transformation (i.e., net N mineralization and net nitrification) rates in one incubation from early July through October 2007 (monsoon season), and a second incubation from October to early July 2008 (winter–spring). We used the resin core method (DiStefano and Gholz 1986), as modified by Kaye and Hart (1998a) for concurrent measurement of net N transformations in the forest floor (O horizon) and mineral soil (0–15 cm). The cores were incubated at a fixed distance (7.5 m) and bearing from the plot center. Net N mineralization and net nitrification in the mineral soil were calculated as the difference between the initial and final mineral soil N pools ($\text{NH}_4^+ + \text{NO}_3^-$ for mineralization; NO_3^- for nitrification) pools plus the $(\text{NH}_4^+ + \text{NO}_3^-)$ -N adsorbed onto the mixed-bed, ion exchange resin (IER) bag fixed beneath the mineral soil. Forest floor net N mineralization and nitrification were estimated similarly by placing a second IER bag on top of the mineral soil core and putting forest floor material on top of this bag. There was not sufficient forest floor material at the wildfire sites to estimate N transformations, but we placed an IER bag on top of the mineral soil to quantify throughfall inputs and be consistent with resin cores in unburned patches (Grady and Hart 2006).

The soils were stored at 4 °C (≤ 5 days) until 30 g of sieved field-moist (< 4 mm) mineral soil were extracted in

Table 1 Burned area and selected mineral soil (0–15 cm) and patch characteristics (mineral soil total C, total N, GWC, and pH; organic horizon C, herbaceous biomass C, and live tree species, density, and basal area) of wildfire chronosequence sites in ponderosa pine (*Pinus ponderosa*) forests of the southwestern US

Time after fire (years)	Patch type	Area burned (ha) ^a	Total C ^b (g m ⁻²)	Total N	GWC ^b (kg H ₂ O kg ⁻¹ soil)	pH ^c	Organic horizon C ^a (g C m ⁻²)	Herbaceous C	Live trees ^d
2	Burned	28	1,898.5 (114.1)	78.7 (6.1)	0.07 (0.10)	5.53 (0.06)	177.2 (58.3)	67.6 (6.1)	PIPO (48, 8)
	Unburned	–	2,404.3 (132.0)	91.4 (6.7)	0.06 (0.01)	5.41 (0.07)	1,403.4 (208.0)	12.6 (4.6)	PIPO (414, 20)
6	Burned	450	2,894.8 (118.0)	156.9 (6.7)	0.12 (0.01)	5.73 (0.09)	291.9 (71.3)	70.5 (8.5)	PIPO (53, 3)
	Unburned	–	2,973.5 (196.1)	128.9 (11.5)	0.09 (0.01)	5.12 (0.09)	2,375.2 (504.7)	2.7 (1.0)	PIPO (782, 46), PIST (48, 1), PSME (80, 7)
7	Burned	268	2,785.2 (62.0)	127.6 (5.7)	0.10 (0.01)	5.55 (0.04)	243.8 (55.3)	59.5 (3.9)	No live trees
	Unburned	–	2,466.1 (168.2)	100.3 (9.5)	0.11 (0.01)	5.04 (0.08)	2,226.1 (375.7)	0.4 (0.2)	PIPO (1160, 47), ROPS (255, 1)
11	Burned	3,495	1,946.5 (224.0)	96.9 (11.5)	0.09 (0.01)	5.58 (0.05)	59.1 (15.1)	54.3 (5.2)	No live trees
	Unburned	–	1,950.3 (222.7)	83.8 (8.7)	0.08 (0.01)	4.97 (0.08)	1,310.6 (170.3)	1.5 (0.7)	PIPO (838, 38)
23 ^e	Burned	1,258	2,804.6 (178.2)	139.8 (10.9)	0.08 (0.01)	5.38 (0.05)	180.7 (66.6)	22.7 (2.7)	PIPO (517, 4)
	Unburned	–	2,178.7 (151.7)	113.0 (7.7)	0.10 (0.01)	5.22 (0.10)	1,915.0 (512.2)	8.5 (3.4)	PIPO (311, 38)
30	Burned	1,858	1,942.2 (72.7)	85.4 (5.4)	0.05 (0.01)	5.71 (0.06)	233.8 (56.7)	19.2 (3.9)	JUDE (223, 1), PIPO (218, 4), QUGA (938, 3)
	Unburned	–	2,846.7 (226.8)	102.4 (10.5)	0.10 (0.01)	5.16 (0.10)	1,029.6 (293.0)	16.5 (7.6)	PIPO (1168, 40)
34 ^e	Burned	3,162	1,851.6 (141.3)	80.5 (5.4)	0.05 (0.01)	5.81 (0.04)	376.6 (127.6)	22.9 (5.8)	PIPO (676, 8)
	Unburned	–	2,156.9 (136.5)	97.3 (9.2)	0.08 (0.01)	5.43 (0.06)	1,556.8 (357.2)	2.9 (1.1)	PIPO (1822, 33)

n = 9 plots/patch; values are untransformed mean ± 1SE

JUDE *Juniperus deppeana* (Steud.), PIPO *P. ponderosa*, PIST *P. strobiformis*, PSME *P. menziesii*, QUGA *Q. gambelii*, ROPS *Robinia pseudoacacia* L.

^a Data are from Ross et al. (2012)

^b GWC gravimetric water content; value is the mean of the July and October 2007 measurements

^c pH measured using 0.01 M CaCl₂

^d Live tree species with density (trees ha⁻¹) and basal area (m² ha⁻¹) in parentheses

^e These burned patches were salvage logged and replanted following the fire

100 mL of 2 M KCl and the IER was extracted in 100 mL of 2 M KCl. We removed items >1 cm in diameter from the forest floor and cut the remainder with scissors and homogenized before extracting 5 g in 25 mL of 2 M KCl. Extracts were mechanically shaken for 1 h, filtered through preleached (with deionized water) Whatman #1 filters, and frozen until they were analyzed for NH_4^+ and NO_3^- on a Lachat AE Flow-Injection Analyzer (Lachat Instruments, Loveland, CO, USA), using indophenol blue (Lachat Instruments, 1990) and cadmium reduction-diazotization (Lachat Instruments, 1992) methods, respectively. The mean bulk density for all four mineral soil cores taken during the study period (2 incubation periods, 1 initial and 1 final for each) was used to convert the mineral soil mass-based transformation rates to an areal basis. Forest floor transformations were converted to an areal basis using the mean bulk density of two 30 × 30 cm quadrats taken at each plot.

We also performed an aerobic laboratory incubation to assess net N transformation rates under constant temperature and moisture conditions. We used mineral soil (0–15 cm depth) from each of the nine plots within each patch ($n = 9$) collected in 2007. Approximately 10 g of air-dried, sieved (<2 mm) soil was placed in a 120-mL glass jar, re-wetted to 60 % water holding capacity (Paul et al. 1999), and incubated at 22 °C for 28 days. Jar lids were loosely sealed to permit air exchange, and distilled water was added as needed to maintain soil water content. Initial and final pools of NH_4^+ and NO_3^- were determined by extracting 10 g of soil in 100 mL of 2 M KCl and analyzing the extracts on a microplate reader (Multiskan EX; Thermo Scientific). The salicylate method was used for NH_4^+ and Devarda's alloy/salicylate method was used for $\text{NH}_4^+ + \text{NO}_3^-$ (Sims et al. 1995); NO_3^- pools were determined by subtracting the NH_4^+ pool from the $\text{NH}_4^+ + \text{NO}_3^-$ pool. Net N transformation rates were calculated as the difference between initial and final inorganic pools ($\text{NH}_4^+ + \text{NO}_3^-$ for mineralization; NO_3^- for nitrification), and expressed as daily rates ($\text{mg m}^{-2} \text{ days}^{-1}$) using the mean bulk density computed previously.

Quantification of gross N transformation rates

We used the ^{15}N isotope dilution method (Hart et al. 1994) to measure gross N transformation rates in a 24-h laboratory incubation. We selected a subset of the burned and unburned chronosequence sites (5 of the 7 original: 2, 7, 11, 30, and 34 years-after-fire) and plots (6 plots per patch) for these measurements to reduce the number of analyses, which are both time consuming and expensive, and still compare older and recent fires. We conducted this measurement in mid-August 2008, because the soil was moist and warm from the summer monsoons, and we expected N

transformations to be maximized during this period (Kaye and Hart 1998b). We also measured soil temperatures at these sites by placing a data logger at each site (Hobo Pendant Data Loggers; Onset Computer, Bourne, MA, USA) at a depth of 5 cm in the mineral soil; values were recorded every 10 s for 3.5 weeks.

We collected mineral soil (0–10 cm) for the gross N transformation incubation on 11, 12, and 13 August 2008 by taking cores with an Oakfield sampler (1.9-cm diameter; Oakfield Apparatus, Oakfield, WI, USA) from a 0.5-m² area at a fixed (7.5 m) distance from the plot center (opposite bearing of the net transformation cores). Soils were kept on ice while in transport and then refrigerated for 24–48 h. We sieved (<4 mm) soils at field-moisture content, and, on 14 August 2008, we weighed approximately 25 g of sieved soil into each of five specimen containers. One sample was used to estimate initial pool sizes of NH_4^+ and NO_3^- while the other four samples were divided into nitrification or mineralization groups at time 0 h (t_0) or time 24 h (t_{24}). We injected 0.35 mL of a labeled solution, $^{15}\text{NO}_3^-$ as $\text{K}^{15}\text{NO}_3^-$ or $^{15}\text{NH}_4^+$ as $(^{15}\text{NH}_4^+)_2\text{SO}_4$ (200 mg N/L; 99 atom % ^{15}N enrichment) uniformly into the appropriate soil using a syringe and needle. The injections added approximately 3.5 mg N/kg dry soil for both of the N species and increased the gravimetric water content (GWC; $\text{kg H}_2\text{O kg}^{-1}$ dry soil) by approximately 7 % on a relative basis (1.7 % absolute change). The t_0 soils were immediately extracted. The t_{24} soils were incubated inside sealed glass Mason jars (~1 L) with distilled water at the bottom to maintain the moisture content for 24 h in the dark at 20 °C. Soils were extracted as described above for in situ net N transformation rates using 100 mL 2 M KCl and frozen until subsequent colorimetric analysis (initial pool sizes) or preparation for ^{15}N analysis.

We performed the ^{15}N analyses using the diffusion procedure described by Stark and Hart (1996). The ^{15}N contents were determined on the diffusion extracts using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer (University of California, Davis, Stable Isotope Facility; PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer; Sercon, Cheshire, UK). We used the NH_4^+ and NO_3^- pool sizes at t_0 and t_{24} , the atom % ^{15}N excess at t_0 and t_{24} , and the equations of Kirkham and Bartholomew (1954) to calculate rates of gross mineralization and nitrification. Rates of NH_4^+ and NO_3^- microbial consumption and were also calculated; however, data are not presented because these rates greatly exceeded gross mineralization and nitrification, which can be an artifact of the ^{15}N isotope dilution technique in N-limited soils (Hart and Myrold 1996). Instead, we estimated gross NH_4^+ assimilation (gross NH_4^+ consumption minus gross nitrification) to gain insights into microbial C and N limitations.

Statistical analyses

We assessed the effects of time-after-fire on net N mineralization and nitrification rates (in situ and laboratory) and initial pools of inorganic N (NH_4^+ and NO_3^- for July and October; where NO_3^- levels were undetectable, we used half the lower detection limit, 0.03 mg N L^{-1}) using linear regression in the burned patches ($n = 7$) and analysis of covariance (ANCOVA) with paired unburned patches as the covariate ($n = 9$ plots per patch). However, neither approach revealed significant temporal trends in the data. Thus, we proceeded to analyze the effects of fire using an ANOVA approach with each site considered a replicate (site = burned and unburned patch; $n = 7$ sites) and t tests to assess fire effects within a site ($n = 9$ plots). In the latter analyses, we recognize that the plots within patches are not independent units, but felt the presentation of data patterns with inferential statistics was of unique and important value (Oksanen 2001). We then assessed changes in net N transformation rates, initial inorganic N pool sizes, and ratios of net nitrification: net N mineralization over time-after-fire using linear regression on the differences between the burned and unburned paired patches (burned – unburned; $n = 7$). This approach accounted for among-site variability and better isolated changes over time after fire. Similarly, we assessed the effect of fire on gross N production rates using ANOVA ($n = 5$ sites), and we analyzed differences (burned – unburned) over time after fire using linear regression on gross N production rates and the ratios of gross nitrification: gross N mineralization. We examined fire effects on the mineral soil characteristics (total C, total N, C:N, pH, and GWC) using one-way ANOVA on the patch means ($n = 7$ sites; pH was analyzed using the hydrogen ion concentration). Finally, we analyzed relationships among net (in situ) and gross N transformations and patch characteristics (listed in Table 1; also average daily soil temperature for gross N transformations) using correlation analysis.

Residuals were visually inspected for each model, and data were transformed as necessary (natural log, square root) to meet the assumptions of ANOVA (normality and homogeneity of variance). Extreme outlier plot values in the net N transformation rates and inorganic N pools were identified as those greater than [the upper quartile + $(3) \times$ (interquartile range)] or less than [the lower quartile – $(3) \times$ (interquartile range)] and were excluded (approximately 1.0 % of the total collected data; Johnson et al. 2010). An a priori alpha level was set at 0.05. All statistical analyses were conducted using JMP statistical software (v.10.0.0; SAS Institute).

Results

Annual in situ net N mineralization rates in burned patches ranged from 3.03 to $6.56 \text{ g N m}^{-2} \text{ years}^{-1}$, which were

lower ($P < 0.01$) than rates in unburned patches (4.35 – $10.36 \text{ g N m}^{-2} \text{ years}^{-1}$; Fig. 1a). Annual net nitrification rates were higher in burned (1.98 – $3.51 \text{ g N m}^{-2} \text{ years}^{-1}$) than unburned (0.15 – $1.87 \text{ g N m}^{-2} \text{ years}^{-1}$) patches ($P < 0.01$; Fig. 1c). Net nitrification accounted for a greater proportion of net N mineralization in burned than unburned patches (mean net nitrification:net N mineralization, burned patches = 0.65 ; unburned patches = 0.19 ; $P < 0.01$; Fig. 1e). We did not include the net N transformation rates in the organic horizon at the unburned patches in the net N transformation rate estimates because most of the apparent net N cycling in the forest floor (net N mineralization: 0.36 – $1.0 \text{ g N m}^{-2} \text{ years}^{-1}$; net nitrification: 0.09 – $0.27 \text{ g N m}^{-2} \text{ years}^{-1}$) was equivalent to the throughfall inputs estimated in burned areas (0.44 – $1.44 \text{ g N m}^{-2} \text{ years}^{-1}$; data not shown). Excluding forest floor net N rates from the analysis did not alter overall patterns between treatments and time-after-fire.

Seasonal patterns of in situ net N mineralization and net nitrification rates in response to fire were similar to those for annual rates, but effects were more pronounced during the monsoon season (Online Resources 1 and 2). Similarly, pools of inorganic N (NH_4^+ and NO_3^-) were higher in burned than unburned patches in July ($P < 0.01$ NH_4^+ and $P = 0.04$ NO_3^- ; Table 2), but differences were less pronounced in October ($P = 0.01$ NH_4^+ and $P = 0.11$ NO_3^- ; Table 2).

The differences in annual in situ net N mineralization rates (burned – unburned) were not significantly correlated with time-after-fire ($R^2 = 0.01$, $P = 0.80$; Fig. 1b), nor were those for annual net nitrification rates ($R^2 = 0.17$, $P = 0.35$; Fig. 1d) or the annual net nitrification:net N mineralization ratios ($R^2 = 0.15$, $P = 0.39$; Fig. 1f). Trends were similar for seasonal rates of net N mineralization, net nitrification, and inorganic N pools (NH_4^+ and NO_3^- ; data not shown).

Daily net N mineralization rates as estimated by the aerobic laboratory incubation did not differ between burned and unburned patches (11 – $183 \text{ mg N m}^{-2} \text{ days}^{-1}$ unburned; 22 – $123 \text{ mg N m}^{-2} \text{ days}^{-1}$ burned; $P = 0.31$; Fig. 2a). Laboratory net nitrification rates were higher in burned (41 – $154 \text{ mg N m}^{-2} \text{ days}^{-1}$) than unburned (-2 to $73 \text{ mg N m}^{-2} \text{ days}^{-1}$) patches ($P < 0.01$; Fig. 2b), but net nitrification:net N mineralization ratios were did not differ between burned (1.2 – 18.1) and unburned patches (0.13 – 3.7 ; $P = 0.10$; Fig. 2c). The differences in laboratory net nitrification (burned – unburned) were negatively correlated to time-after fire ($R^2 = 0.80$, $P = 0.01$), but those for net N mineralization and net nitrification : net N mineralization ratios were not ($R^2 = 0.01$, $P = 0.87$ and $R^2 = 0.32$, $P = 0.18$, respectively; Online Resource 3).

Gross N mineralization rates did not differ between burned and unburned patches (7.3 – $86.0 \text{ mg N m}^{-2} \text{ days}^{-1}$

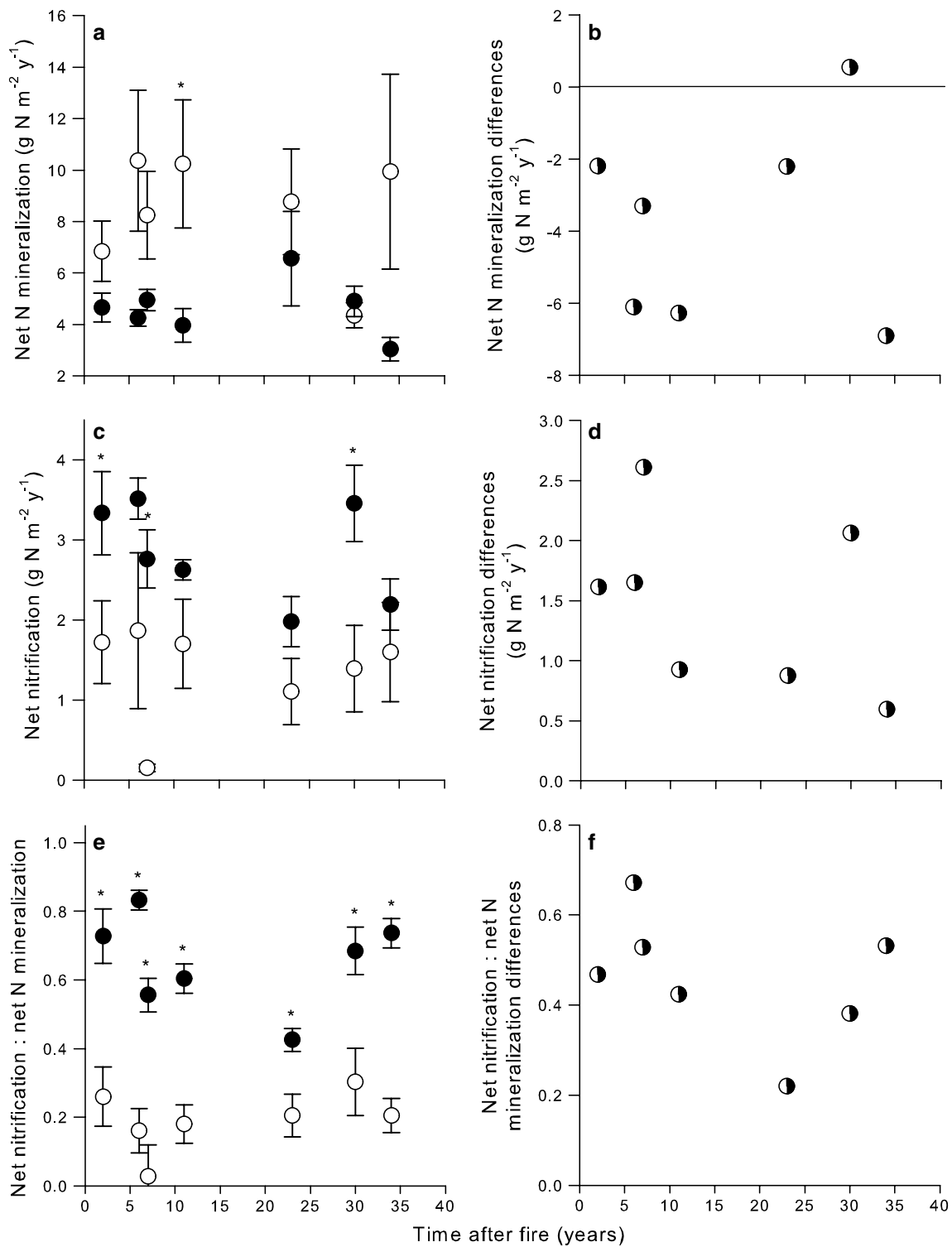


Fig. 1 Annual net N mineralization (a) and net nitrification (c) rates in mineral soil (0–15 cm) measured in situ at seven burned patches (filled circles) and adjacent unburned patches (open circles) at wild-fire chronosequence sites in ponderosa pine (*Pinus ponderosa*) forests of the southwestern US (means $\pm 1 \text{ SE}$; $n = 9$ plots within a patch; note different scales in y axes). **e** Ratio of net nitrification to

net N mineralization in burned and unburned patches. **b, d, f** Differences (semi-filled circles) between burned and unburned patches for respective rates or ratio. Differences ($P < 0.05$) between paired burned and unburned patches are noted (asterisk). Burned patches 23 and 34 years-after-fire were salvage logged and replanted

Table 2 Initial inorganic N (NH_4^+ and NO_3^-) pool sizes (g N m^{-2}) for July (monsoon measurement) and October (winter-spring measurement) at wildfire chronosequence sites in ponderosa pine forests of the southwestern US

	Time after fire (years)	Patch type	July		October	
			NH_4^+	NO_3^-	NH_4^+	NO_3^-
Unique letters within pools, months, and years indicate significant differences between burned and unburned patches ($P < 0.05$)	2	Burned	0.32 (0.07) a	0.63 (0.37)	0.20 (0.02) a	0.58 (0.23)
		Unburned	0.13 (0.02) b	0.01 (0.01)	0.08 (0.01) b	0.03 (0.01)
	6	Burned	0.14 (0.02) a	0.03 (0.02)	0.16 (0.02) a	0.03 (0.01)
		Unburned	0.05 (0.02) b	0.01 (0.001)	0.08 (0.02) b	0.01 (0.002)
	7	Burned	0.16 (0.02) a	0.05 (0.02)	0.08 (0.02)	0.06 (0.01)
		Unburned	0.02 (0.01) b	0.01 (0.002)	0.05 (0.01)	0.02 (0.01)
	11	Burned	0.20 (0.03) a	0.05 (0.02)	0.11 (0.02) a	0.04 (0.01)
		Unburned	0.10 (0.02) b	0.02 (0.002)	0.06 (0.01) b	0.02 (0.01)
	23 ^a	Burned	0.19 (0.03) a	0.02 (0.001)	0.10 (0.01)	0.10 (0.02)
		Unburned	0.09 (0.01) b	0.01 (0.001)	0.06 (0.01)	0.11 (0.02)
	30	Burned	0.22 (0.03)	0.10 (0.03)	0.13 (0.02)	0.03 (0.01)
		Unburned	0.14 (0.05)	0.04 (0.02)	0.10 (0.03)	0.04 (0.02)
^a These burned patches were salvage logged and replanted following the fire	34 ^a	Burned	0.17 (0.03) a	0.01 (0.002)	0.08 (0.01) a	0.03 (0.01)
		Unburned	0.07 (0.01) b	0.01 (0.001)	0.06 (0.01) b	0.02 (0.001)

unburned, -25.5 to $79.4 \text{ mg N m}^{-2} \text{ days}^{-1}$ burned; $P = 0.67$; Fig. 3a). Gross nitrification rates were higher in burned patches (31.5 – $121.4 \text{ mg N m}^{-2} \text{ days}^{-1}$) than unburned patches (6.7 – $29.0 \text{ g N m}^{-2} \text{ days}^{-1}$; $P < 0.01$; Fig. 3b), as were the ratios of gross nitrification to gross N mineralization ($P = 0.04$; Fig. 3c), excluding the year 34 site, where the ratio could not be calculated because the gross N mineralization rate was very close to zero. The differences between burned and unburned rates of gross N mineralization and nitrification were not correlated with time-after-fire ($R^2 = 0.22$; $P = 0.43$; $R^2 = 0.01$; $P = 0.87$, respectively; data not shown), nor were the differences in the ratio of gross nitrification rates to gross N mineralization ($R^2 = 0.68$, $P = 0.18$; data not shown). Gross NH_4^+ assimilation rates were higher in unburned patches than burned patches ($P = 0.01$; Online Resource 4).

Soil pH was higher in burned patches (5.53 – 5.81) than unburned patches (4.97 – 5.41 ; $P < 0.01$), and average daily soil temperatures over the 3.5-week period during the monsoon season were approximately 4°C warmer in burned than unburned soils (14.4 and 18.7°C , respectively; $P < 0.01$). Other mineral soil characteristics (total C and N; carbon-to-nitrogen mass ratio, and GWC) did not differ between burned and unburned patches. Organic horizon C, herbaceous C, aboveground live tree C, and soil pH were correlated to annual net N mineralization ($r = 0.82$, $P < 0.01$; $r = -0.71$, $P < 0.01$; $r = 0.77$, $P < 0.01$; $r = -0.69$, $P < 0.01$, respectively) and nitrification ($r = -0.79$, $P < 0.01$; $r = 0.77$, $P < 0.01$; $r = -0.77$, $P < 0.01$; $r = 0.73$, $P < 0.01$, respectively), while organic horizon, aboveground live tree C, and average daily soil temperature were correlated to gross nitrification rates

($r = -0.73$, $P = 0.02$; $r = 0.74$, $P = 0.01$; $r = 0.73$, $P = 0.02$, respectively). None of the variables were related to gross N mineralization rates.

Discussion

Stand-replacing wildfires had persistent, long-term effects on net and gross nitrification rates and inorganic N pools and, quite notably, all these components of N cycling lacked a significant time-after-fire trend over the course of more than three decades. Current knowledge of post-fire N cycling suggests that N availability is stimulated by fire disturbance, but the effects are short term (Raison 1979; Covington and Sackett 1992; Wan et al. 2001) and decline over the course of secondary succession (Vitousek et al. 1989). Based on this prior research, we hypothesized that net N transformations, inorganic N pools, and gross nitrification rates would gradually become similar to comparable unburned forest over time after fire. Instead, our observations of elevated N availability and nitrification rates following stand-replacing wildfire in southwestern ponderosa pine forests indicate that this type of wildfire is not a “pulse” but rather a “press” type disturbance (i.e., a sustained alteration; Bender et al. 1984). High rates of nitrification were sustained over time, and, as we predicted, the effects were more pronounced during the monsoon season, and nitrification comprised a greater proportion of net N mineralization in burned patches. Overall, these findings suggest that stand-replacing wildfires in these ecosystems trigger an N cycling state shift.

Shifts to alternative states are generally caused by stochastic disturbance events that push an ecosystem beyond

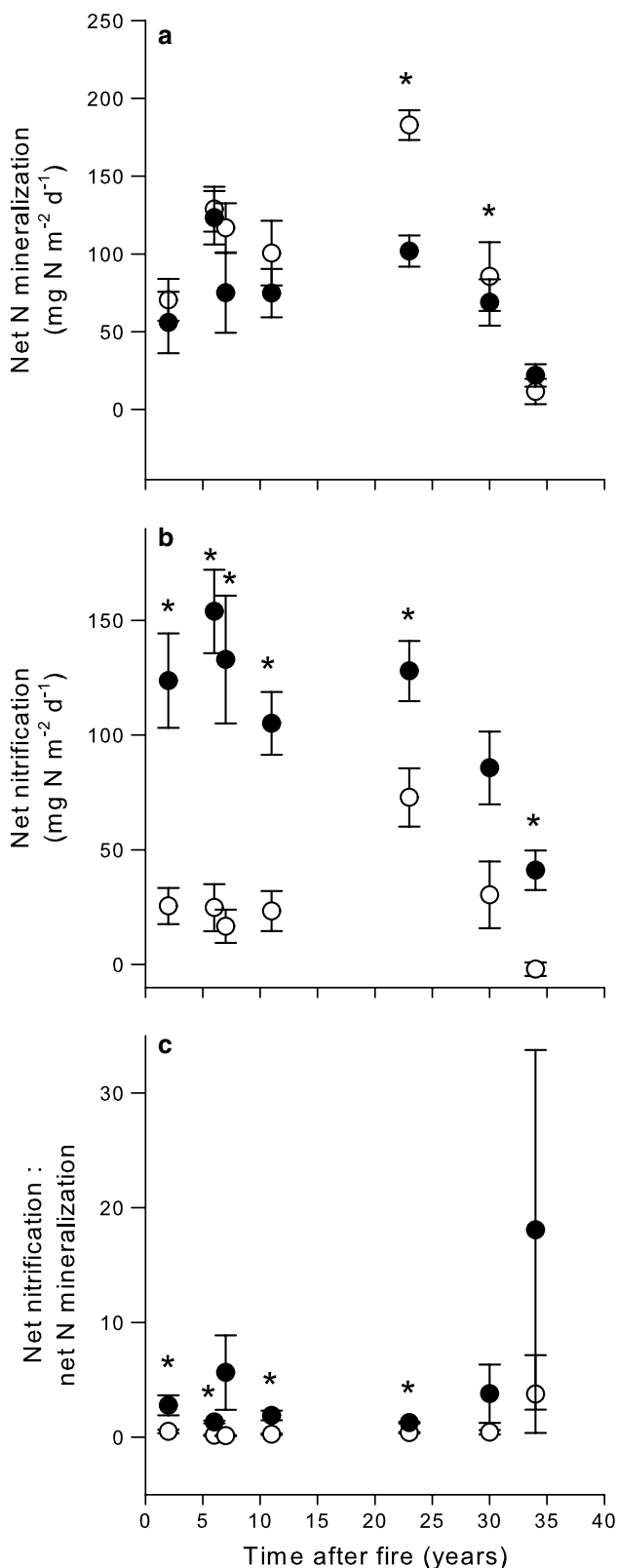


Fig. 2 Daily net N mineralization (**a**) and nitrification (**b**) rates measured in a 28-day aerobic laboratory incubation using mineral soils from seven burned patches (filled circles) and adjacent unburned patches (open circles) at wildfire chronosequence sites in ponderosa pine forests of the southwestern US (means \pm 1SE; n = 9 plots within a patch; note different scales in y axis). Differences (P < 0.05) between paired burned and unburned patches are noted (asterisk). **c** Ratio of net nitrification to net N mineralization for burned and unburned sites at each year. Burned patches 23 and 34 years-after-fire were salvage logged and replanted

as the maximum amount of disturbance that an ecosystem can endure without pushing it into an alternative state, and management activities, such as fire suppression, can inadvertently diminish resilience by reducing ecosystem diversity in time and space (Holling 1973; Peterson et al. 1998). Southwestern ponderosa pine forests typify this model because management, including the introduction of cattle grazing and active fire suppression, has had the unintended consequence of homogenizing these forests into dense stands of small-diameter trees, which are very susceptible to stand-replacing wildfires (Covington and Moore 1994). Effectively, human activities over the last ~100 years have reduced the ecological resilience of these forests; thus, fire, which was previously an integral and renewing component of the disturbance regime, is now an agent capable of pushing these forests into alternative stable states (Nyström et al. 2000; Savage et al. 2013). Our research suggests that stand-replacing wildfire disturbance in these ecosystems initiates a shift from low to high nitrification rates, and this shift may be reinforced by various biological (microbial and plant communities), physical (soil temperature and presence of charcoal), and chemical (soil pH) feedbacks.

Changes in soil pH, temperature, and the presence of charcoal may be responsible for the prolonged maintenance of elevated nitrification rates in burned soils. Post-fire increases in soil temperature and pH favor nitrifier activity (Christensen 1973; Bauhus et al. 1993); consistent with these previous findings, we observed positive correlations between net nitrification rates and soil pH and gross nitrification rates and average daily soil temperatures. However, warmer soils in the burned patches are probably not the primary mechanism driving high nitrification rates, because we also observed high net nitrification in these soils under aerobic laboratory conditions. Nitrification can also be enhanced by fire-produced charcoal (DeLuca and Sala 2006), either through the sorption of inhibitory phenolic compounds (Zackrisson et al. 1996) or by increasing microbial activity (Pietikäinen et al. 2000).

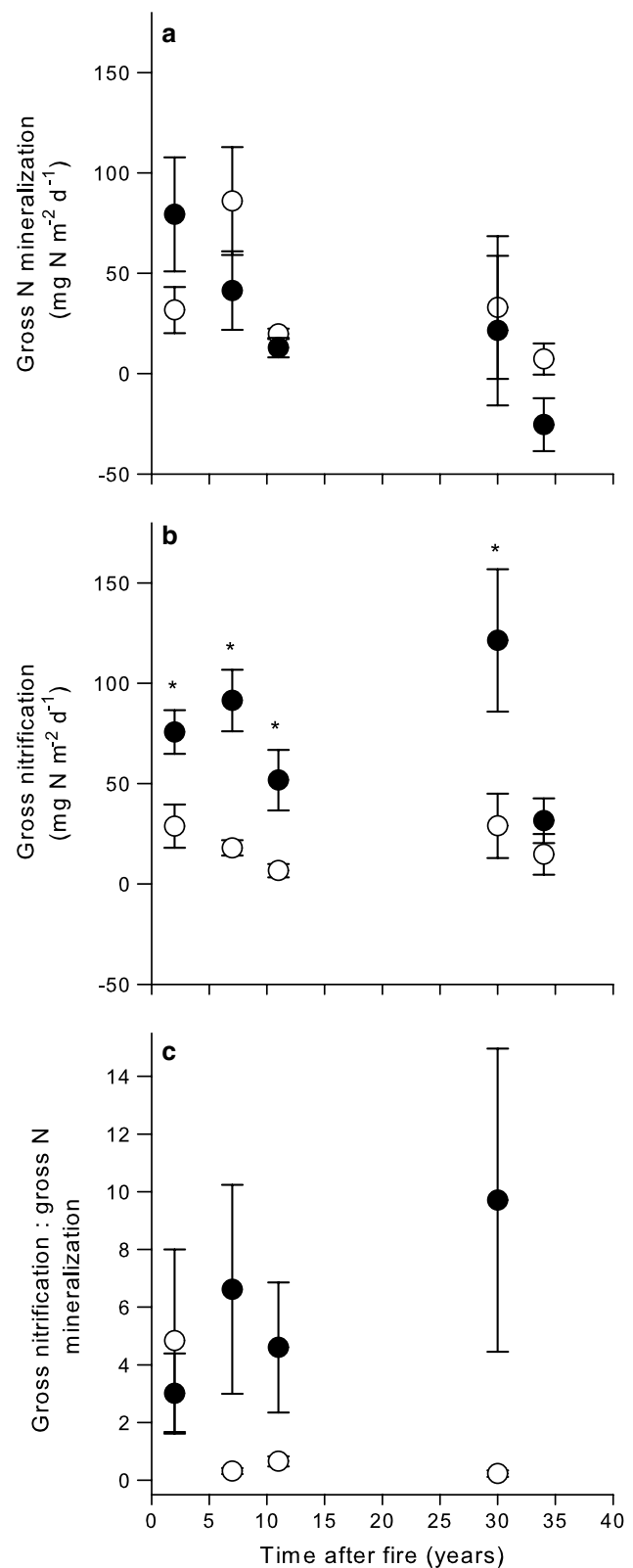
Nitrification in burned soils may also be perpetuated by changes in the aboveground vegetation; in particular, the herbaceous vegetation that predominates recently burned areas (Laughlin et al. 2010). Post-fire, microbial-mediated ecosystem processes are thought to be driven by the

a given threshold, and the alternative state is stabilized by a variety of feedback mechanisms (Scheffer et al. 2001). Contemporary perspectives on ecological resilience view it

Fig. 3 Daily gross N mineralization (a) and nitrification (b) rates measured by ^{15}N isotope dilution technique in a 24-h laboratory incubation using mineral soils from five burned patches (filled circles) and adjacent unburned patches (open circles) at wildfire chronosequence sites in ponderosa pine forests of the southwestern US (means \pm 1 SE; $n = 6$ plots within a patch). Differences ($P < 0.05$) between paired burned and unburned patches are noted (asterisk). c Ratio of gross nitrification to gross N mineralization for burned and unburned sites; note that a ratio could not be calculated for year 34 site because gross N mineralization was approximately zero. Burned patches 23 and 34 years-after-fire were salvage logged and replanted

vegetation trajectory (Hart et al. 2005), and net N transformation rates tend to be higher in grass openings than under pine trees in southwestern ponderosa pine forests (Kaye and Hart 1998a). If burned sites become re-vegetated, we expect plants, especially trees, to compete more effectively for N against heterotrophic microbes (Johnson 1992). Although we observed a positive association between herbaceous C and net nitrification rates, herbaceous vegetation only accounted for a dominant portion of the total plant biomass at some of the recently burned patches (100 % at 7 and 11 years-after-fire; 26 % at 6 years-after-fire; 3 % at 2 years-after-fire, which was dominated by one exceptionally large living tree), and it comprised only 2–5 % of the total plant biomass at the three oldest burns (Ross et al. 2012). This implies that the persistent post-fire pulse of nitrification that we observed may not be entirely a grass-dependent condition. Overall, low levels of live plant biomass in burned patches compared to unburned patches (Ross et al. 2012) suggests that low plant N uptake helps maintain post-fire nitrification rates, and, indeed, high rates of net nitrification have been reported for unvegetated microsites in lodgepole pines forests (Metzger et al. 2008). Reduced NH_4^+ uptake by plants would allow autotrophic nitrifying bacteria or archaea to better compete for NH_4^+ substrate, thus promoting greater nitrification (Kaye and Hart 1997).

If the presence of grasses or low tree N uptake are mechanisms that maintain high nitrification in soils, then nitrification may be maintained indefinitely by the slow and unpredictable natural tree regeneration in these forests. Post-fire vegetation trajectories in ponderosa pine forests are varied, including grassland, shrubland, or dense forest (Savage and Mast 2005; Roccaforte et al. 2012), and natural regeneration is limited by the need for a specific combination of seed production, weather conditions, and a favorable seedbed (Heidmann 2008). Cone production in ponderosa pine is enhanced by N fertilization (Heidmann 1984), so it may be facilitated following wildfire. However, the widespread fire-induced pine mortality would likely pose a significant barrier to natural regeneration because conifer regeneration is most limited by the distance to the nearest seed-bearing tree (Bonnet et al. 2005). Additionally, seedling establishment may depend on various other



factors, including soil moisture conditions (Savage et al. 2013), fire severity (Crotteau et al. 2013), and specific mycorrhizal linkages (Booth and Hoeksema 2010).

Overall, pools of inorganic N were higher in burned than unburned patches. Although it is difficult to directly resolve whether this due to higher gross production, reduced microbial consumption, or a combination of the two, the unburned patches had higher gross NH_4^+ assimilation rates than the burned patches. This is presumably because greater C availability in the unburned patches led to greater NH_4^+ assimilation. Consistent with this, previous work at these study sites documented lower labile C concentrations in the mineral soil of burned patches, such that soil CO_2 efflux was lower in burned patches during the monsoon season (Ross et al. 2012). Also, in a similar forest type, Koyama et al. (2010) attributed higher NO_3^- pools in burned soils to reduced microbial uptake, most likely due to C-limiting conditions produced by fire (2 years previous). We suspect that persistent C limitations caused lower microbial assimilation of NH_4^+ in burned soils, thus increasing the availability of NH_4^+ substrate for nitrification. This higher substrate availability, coupled with lower plant N uptake, may offer nitrifiers a competitive advantage in burned soils and lead to higher net and gross nitrification rates.

The high nitrification rates that we observed in burned patches are consistent with those found beneath herbaceous vegetation in similar forests that were restored to emulate presettlement structure (Kaye and Hart 1998a). This implies that stand-replacing wildfires may have caused nitrification to return to rates associated with the open canopy forest structure that prevailed under the presettlement, low-intensity surface fire regime (Hart et al. 2005). The similarities in N cycling between current burned forests and presettlement herbaceous patches argue that the elevated nitrification rates we observed may be stable over time. Over the long term, areas directly beneath trees may revert back to lower nitrification rates, as evidenced by the negative associations we observed between net and gross nitrification rates and live tree biomass and organic horizon C. However, it is unlikely that trees will regenerate to the same density as current unburned forests under future climate scenarios (Roccaforte et al. 2012), so it is likely that sustained nitrification rates will continue to persist.

We note that the ratios of nitrification:N mineralization were generally higher for the laboratory-determined N transformation rates (gross and net) than those determined in situ. This may have resulted from using field-incubated, intact cores for the in situ measurements and sieved soils for the laboratory incubations. Nitrogen transformation rates measured in mixed soils are not necessarily representative of those in undisturbed soils (Booth et al. 2006). In our study, sieving may have increased substrate (NH_4^+) availability to nitrifiers, and, thus, stimulated nitrification rates to a higher degree in the laboratory-based measurements. This may also explain why rates of gross

nitrification tended to be higher than those of gross N mineralization. In addition, we note that laboratory-based net rate estimates of N transformations were higher than those for gross rates. The use of air-dried soil for the net rates may have stimulated N transformations because soils were re-wetted to 60 % of their water holding capacity (to ~0.34 GWC) prior to incubation, whereas field moist soil (~0.25 GWC) was used for gross rates. Thus, the two laboratory-based measurements represent potentials of N transformations under different moisture histories.

Conclusions

The N cycling of southwestern ponderosa pine forests that historically experienced frequent, low-intensity surface fires is fundamentally altered by the occurrence of stand-replacing wildfires. Our net and gross N transformation rate measurements demonstrate a post-fire increase in nitrification that extends for more than three decades. These findings advance previous knowledge of fire and ecosystem ecology by demonstrating that high nitrification rates are not necessarily a short-term response to fire, nor are they entirely an herbaceous vegetation-dependent condition. We suggest that stand-replacing wildfire in southwestern ponderosa pine forests leads to an N cycling state shift, from low nitrification in unburned patches to high nitrification in burned patches. This biogeochemical state shift signifies a “press” type disturbance that may be maintained by limited tree regeneration and the presence of herbaceous vegetation and fire-deposited charcoal.

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